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COMPARATIVE ANATOMY OF THE NORMAL AND DISEASED ORGANS OF ABIES BALSAMEA AFFECTED WITH ÆCIDIUM ELATINUM.

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(WITH PLATES XIV AND XV)

I. INTRODUCTORY.

WITHIN the last few years some attention has been given to the study of the deformations and anatomical changes that take place in plants when attacked by parasitic fungi. Such changes become more marked when the relations between host and parasite are such that there exists a sort of mutualism between the two. In many cases the hypertrophied organs of the host plant lose their photosynthetic power, and thus, by assuming parasitism, become more dependent on the normal parts of the host for their existence. This is always true of the so-called "witch brooms" (Hexenbesen) on species of Abies affected with *Æcidium elatinum*. Here the affected and hypertrophied part of the plant becomes a morphological unit, the anatomy and physiology of which departs from that of its normal homologues.

The anatomy of different species of Abies varies slightly under normal conditions. This is especially true of the leaves and younger branches, which in some species have tissues and

structures that may be rudimentary or wanting in others.   Such structural and anatomical diversity either becomes more marked, or is entirely lost in hypertrophied or atrophied organs.

The deformations and anatomical changes resulting in the hypertrophied branches of *A. pectinata*, affected with *Æ. elatinum*, were first described in a general way by De Bary[1] who demonstrated that the "witch broom" was caused by a fungus.

Later, Hartmann[2] made a comparative anatomical study of the diseased and the healthy leaves and branches of the same witch broom.   The writer[3] has made a comparative study of the diseased and the healthy buds of *A. pectinata*, as well as the formation and distribution of the abnormal resin canals that are formed in the wood of the branches affected with the same fungus.   By comparing the witch broom of *A. firma* Siebold of Japan with that of *A. pectinata*, it was found that differences occur in the two, depending largely upon the differences existing in the normal leaves and branches of the two mountain species of Abies.

According to the analyses of Mayr,[4] the wood of *A. pectinata* contains the least per cent. of resin of any of the cultivated firs. *A. balsamea* differs from *A. pectinata* and *A. firma*, not only in its specific characters and peculiarities, as a large resin or balsam producer, but also in being a swamp species.   For this reason, as well as its being exclusively an American species, one would expect to find marked structural and anatomical changes in the affected leaves and branches.   The anatomy of the *Æ. elatinum* witch broom of *A. balsamea* has not been studied.

For the purpose of making a comparative anatomical study of this witch broom, material was collected from trees growing in a bog near Walker, on Leech lake, northern Minnesota, September 1896.

[1] DE BARY : Ueber den Krebs und die Hexenbesen der Weisstanne.   Bot. Zeit. 1867.

[2] HARTMANN, F : Anatomische Vergleich der Hexenbesen der Weisstanne mit den normalen Sprossen derselben.   Inaug. Diss. Univ. Freib. 1892.

[3] Ueber abnorme Bildung von Harzbehältern und andere zugleich auftretende anatomische Veränderungen in Holze erkrankter Coniferen.   Inaug. Diss. Univ. München, 1896.

[4] MAYR, HEINRICH : Durability of resinous woods.   Pop. Sci. Monthly **28** : 680.

II. GENERAL CHARACTERS OF THE WITCH BROOM.

Æ. elatinum Alb. & Schw. usually attacks the younger lateral branches of *A. balsamea* (L.) Mill. which take the infection either in the young shoots, or in the wounded bark of older ones. Branches over five years old seldom take the infection, differing in this respect from *A. pectinata*, which often has large swellings on the older branches and on the main trunk, due to this disease. It often happens that the terminal shoot becomes diseased, in which case the whole tree soon dies from insufficient light, not being able to increase in height fast enough to keep out of the shade of surrounding trees.

The irritation due to the fungus mycelium causes an increased growth of the bark and wood at the first point of infection, producing a so-called "boil" or tumor on the diseased branch. This tumor is always present and increases in diameter with the increase in age of the witch broom. The diseased annual shoot is shorter, but has a greater diameter than the normal.

Owing to the development of a greater number of the latent and lateral buds of the affected branches, the number of the diseased branches above the normal is greatly increased. In this way a sort of broom is formed. The leaves of the diseased branches spread on all sides like the leaves of the erect terminal shoots. This is partly due to the fact that the terminal as well as the diseased branches are all negatively geotropic, unlike the normal lateral branches which are diageotropic. On account of the absence of chlorophyll the diseased leaves have a yellowish color. The leaves of the diseased branches are about one half as long as the normal leaves of the lateral branches, but they are usually of the same length as the leaves of the normal terminal shoots. The normal leaves of the lateral branches are arranged nearly in one horizontal plane, not because the phyllotaxis is altered, but because the leaves are twisted more or less at the base, just above the pulvinus. It is easy, therefore, to distinguish between the normal and diseased branches, the normal ones always having this apparent distichous leaf arrange-

ment, while in reality they are still polystichous, like the leaves on the terminal shoot.

The *Æ. elatinum* witch broom on *A. balsamea* differs from that found on *A. pectinata* and *A. firma*, in that it seldom has normal branches growing together with the diseased ones above the tumor. The diseased branches are also more numerous, but correspondingly smaller. With the increase in height of the tree, the lower normal branches and the affected branches soon die on account of an insufficient amount of light. The witch broom dies with them, since it is dependent on the normal host for its food supply.

Although that part of the witch broom branch below the tumor is not diseased, its annual growth in diameter is less than in normal branches of the same age. The supply of food is transported to the witch broom, which grows at the expense of the normal parts of the host. This increased growth of the witch broom makes it much heavier than the normal branches, so that it is usually found suspended from larger limbs of the tree, or hanging near the tree trunk when the whole branch is affected. The living and actively growing ones on older trees, excepting where the trees are isolated, are always found near the top, where there is a sufficient food supply. Although photosynthesis is almost entirely absent in the witch broom, it is extremely sensitive, and dies from an insufficient amount of light.

As to the size of the witch broom on *A. balsamea*, the average diameter is from 15 to 30^{cm}, and the length from 20 to 60^{cm}.[5]

III. ANATOMY OF THE NORMAL AND DISEASED LEAVES.

1. *Normal leaves.*—The leaves of Abies are sessile, and without the prominent pulvini peculiar to the spruces. The leaves of the lateral branches of *A. balsamea* are more or less flattened, notched, or obtuse at the tip, grooved on the upper surface and

[5] *Picea nigra*, which grows with *A. balsamea* in the bogs of northern Minnesota, often has a witch broom 40 to 90^{cm} in diameter. The broom is caused by an increase in the number of branches, the internodes of which remain shorter than in the normal. This witch broom is not caused by *Æ. elatinum*, but by some other fungus or insect (Compare v. Tubeuf, Forst-naturw. Zeitsch. —:76. *pl. 5.* 1893.

with a somewhat prominent midrib or keel below. They are always twisted at the base, giving them the distichous direction peculiar to species of Abies. The leaves on the erect shoots are not transversely heliotropic, or twisted at the base, but grow in all directions from the shoot. They are shorter and thicker than those of the lateral branches, more or less awl shaped, and are sharply pointed at the tip.

The number and arrangement of the stomata seem to vary in different localities. Masters[6] finds that the stomata are chiefly on the upper surface of the leaf. McNab[7] in his description gives two or more rows of stomata in the middle line near the apex on the upper surface, with two or more rows on each side of the midrib on the lower surface. Bastin and Trimble[8] find the greater number on the lower surface. I find that by far the greater proportion of the stomata are on the lower surface of the leaves of the lateral branches, which have one band of from 3 to 10 rows on the upper surface, and two bands of 8 to 10 rows on each side of the midrib on the lower leaf surface. On both surfaces the stomata are found in greater numbers toward the apex of the leaf. The more or less terete leaves of the terminal shoots have their stomata distributed about equally on all sides.

Cross sections of the leaves show a well marked cuticle covering the lignified epidermal cells, the outer walls of which are cuticularized and much thickened. Immediately under the epidermis lies the hypoderm when present (*fig. 1*). As to the presence or absence of a hypoderm, McNab[9] says that it is wanting. Engelmann[10] found that the leaves have scarcely any hypoderm cells above, and very few on the edges and keel, fewer than any other species of Abies. Sometimes no hypodermal cells

[6] MASTERS, M. T.: Anatomy and life-history of the Coniferæ. Jour. Linn. Soc. 27 : 250.

[7] McNAB: New way of determining species of Abies. Robinson, The Garden 11 : 280.

[8] BASTIN and TRIMBLE: A contribution to the knowledge of some North American Coniferæ. Am. Jour. Pharm. 68 : 556.

[9] *Ibid.*, p. 280.

[10] ENGELMANN, G.: The American firs. Gard. Chron. N. S. 9 : 300. 1878.

were found.   Bastin and Trimble[11] observed no hypoderm except
along the midrib on the lower leaf surface.   The presence or
absence of strengthening, or hypodermal cells, however, depends
entirely on the part of the leaf from which the cross sections
are made.   Hypoderm cells rarely occur in cross sections made
above the middle of the leaf, while below the middle they are
always present.   Thus, numerous cross sections at five different
parts of the leaves show in the following table their distribution
(see page 315).

Longitudinal sections of the leaves show that the thick-
walled hypodermal cells are long and bast-fiber like, with taper-
ing, oblique, or blunt ends.   The isolated cells are tapering at
their upper ends and extend farthest up into the leaf.   Their
function, as is well known, is for strengthening the leaves.   The
leaves on the terminal shoots are much more rigid than the leaves
on the lateral branches.   This is due to the greater development
of their hypoderm.   Like the epidermal cells they are lignified.
The walls are unequally thickened and often provided with
pore canals.   In *A. balsamea* one never finds them extending into
the mesophyll, as they do in the leaves of *A. firma*.   The num-
ber of hypodermal cells decreases from the base toward the tip
of the leaf; but with the decrease in the number of hypodermal
cells there occurs a corresponding increase in the number of
stomata.

The mesophyll, which forms the chief substance of the leaf
within the hypoderm, agrees in its main characteristics with that
found in the leaves of most species of Abies.   The two dis-
tinct layers of palisade cells extend around the rounded angles
of the leaves.   In the center of the mesophyll, and midway
between the endoderm and outer angles of the leaf, lie the two
circular resin canals, which are large in *Abies balsamea*.   The
resin canals are lined with the thin walled epithelial cells, which
are themselves surrounded by one layer of thick-walled strength-
ening cells.   These strengthening cells differ from the sub-
epidermal ones in that they are shorter and not fiber-like.

[11] *Ibid.*, p. 556.

TABLE I.

CROSS SECTIONS OF LEAVES OF A. BALSAMEA, SHOWING THE DISTRI-
BUTION OF THE HYPODERMAL STRENGTHENING CELLS.

	Cross sections	Leaves of lateral branches	Leaves of terminal shoots
One millimeter above the base.	1. Upper surface. (Ventral.)	Hypodermal layer continuous, except where it is perforated by the stomata.	Hypodermal layer unbroken; often with double rows of cells.
	2. Lower surface. (Dorsal.)	Like 1. Layers often double at the midrib.	Like 1. Often with 2 to 4 rows of cells at the midrib.
	3. At the angles.	Single hypodermal layer unbroken.	Hypodermal layer consisting of 2 to 3 rows of cells.
Half way between middle and base.	1. Upper surface.	Hypodermal cells present, but more or less isolated.	Hypoderm unbroken, often double rowed.
	2. Lower surface.	Like 1, but more numerous, forming a continuous layer at midrib.	Like 1, often with three rows at midrib.
	3. At the angles.	Like 1.	Layer continuous, often double rowed.
At the middle.	1. Upper surface.	Hypodermal cells seldom present.	Hypodermal layer often broken by mesophyll and stomata cells.
	2. Lower surface.	Like 1. Single layer often continuous at the midrib.	Like 1, but never broken at the midrib where it is often double.
	3. At the angles.	Like 1.	Hypoderm unbroken.
Half way between middle and apex.	1. Upper surface.	Hypoderm wanting.	Hypodermal cells isolated when present.
	2. Lower surface.	Usually 2 to 5 strengthening cells at the midrib.	Hypoderm continuous at midrib. At other parts, cells isolated.
	3. At the angles.	Hypoderm wanting.	6 to 10 cells present in one continuous layer.
One millimeter below apex.	1. Upper surface.	Hypoderm wanting.	Hypodermal cells scattered and isolated when present.
	2. Lower surface.	Hypoderm wanting.	Like 1, but with a continuous layer of 8 to 15 cells at the midrib.
	3. At the angles.	Hypoderm wanting.	2 to 5 hypodermal cells usually present.

The elliptical endoderm or bundle sheath, which lines the mesophyll on its inner side, separating it from the central pericycle and fibrovascular bundle, consists of one very distinct layer of large, usually oval, non-lignified parenchyma cells.

The pericycle consists of more or less thickened, lignified parenchyma cells, destitute of chlorophyll. The greater part of it lies on the dorsal side of the leaf, while the vascular bundle occupies the ventral. The pericycle consists of two kinds of cells, forming two distinct areas. First, a central, well marked area with non-pitted cells, varying greatly in size and in the thickness of their cell walls (*fig. 2*). These cells separate with 2 or 3 layers the two divisions of the vascular bundle in the middle part of the leaf, where the bundle is bifurcated. They extend up into the ventral or xylem side of the bundle, forming a wedge shaped area of thick walled cells. On the phloem side they are thinner walled, but larger, and fill up the whole center of the pericycle, extending dorsally to the endodermis in the leaves of the lateral branches. But in the leaves of the terminal shoots, the non-pitted area is separated from the endodermis by a layer of the pitted parenchyma. Second, the pitted parenchyma of the pericycle, which forms the so-called transfusion tissue of von Mohl. This part consists of linear lignified cells with bordered pits on their ends, as well as on their lateral walls (*fig. 3*). The transfusion tissue is not as well developed in the leaves of the lateral branches as in the leaves of the terminal shoots. In the former there are two small areas, each one lying dorsal to the outer half of the two phloem areas. Each area of the transfusion tissue extends along the endoderm about one-eighth of its circumference. In the leaves of the terminal shoots the two parts of the transfusion tissue begin at the outer edges of each of the phloem parts and follow the endodermis until they meet, thus making a semicircular area of transfusion tissue, 2 to 6 cells deep on the dorsal side of the leaf beneath the endodermis. More than one-half of the pericycle of the leaves of the terminal shoots consists of transfusion tissues.

The vascular bundle lies near to the endoderm on the ventral

side of the leaf.   At the base and apex of the leaf the bundle is undivided; but in the middle, and for the greater part of its length, it is bifurcated.   The phloem part (dorsal) consists of smaller and less thickened cells than those of the xylem (ventral).   The phloem and xylem cells are arranged in more or less distinct rows, usually separated by medullary rays.   The cells of the medullary rays frequently contain crystals of calcium oxalate.

2. *Diseased leaves.*—The diseased leaves are about one-half to three-fourths as long as the normal ones on the lateral branches, but they have about the same length and thickness as the leaves of the terminal shoots.   The diseased leaves growing, as they do, on negatively geotropic branches, are more or less homologous to the normal leaves of the terminal shoots.   In comparing the anatomy of the diseased and the healthy leaves, those of the lateral shoots should be considered.   In Hartmann's comparative anatomical study of the witch broom of *A. pectinata* the leaves of the lateral branches only are considered. The cuticle of the diseased leaves is less thickened than that of the normal leaves.   The number of stomata and stomatal rows varies according to the size of the leaf, as well as to the severity of the mycelial infection.   There are only about one-half as many stomata in the diseased as in the normal leaves.

The epidermal cells vary greatly in size; they have larger lumina than the normal and are less thickened, especially on their inner sides, which are seldom laminated, or provided with pore canals.   The hypodermal cells are present, especially in the basal half of the leaf.   They are more irregularly distributed, often forming nests and groups.   The cells are often twice as large and thick walled as the normal hypodermal cells (*fig. 4*). As in the normal leaves, the number of hypodermal cells decreases from the base toward the apex, but with the decrease in the number of hypodermal cells an increase takes place in the number of stomata on the upper and lower leaf surfaces.   On account of the unequal thickening and irregular distribution of their epidermal and hypodermal cells, the diseased leaves shrivel

up on drying, soon after the ripening of the æcidia. The epidermal and hypodermal cells are lignified.

The mesophyll is made up of a mass of large, irregular cells, with large intercellular spaces. There is no differentiation into palisade tissue and spongy parenchyma. The fungus mycelium is found in all the cells and intercellular spaces. The two resin canals are also present in the diseased leaf. Their epithelial cells are usually larger and more irregular than the normal. The strengthening cells are not thickened, hence the resin canals become irregular in form and size, and often lose their identity in older leaves.

The endoderm is seldom distinguishable as such, its cells forming no ring.

The two lignified parenchyma areas of the pericycle are well defined, especially at the basal portion of the leaf. The transfusion tissue is nearly always present, often in one to three small areas on the dorsal side of the phloem part of the vascular bundle. In well developed leaves, especially in sections made near the base, the transfusion tissue fills up more than one-half of the pericycle. It is unlike the pitted parenchyma of the normal pericycle, in that its cell walls have simple as well as bordered pits. The cells are also irregular in form, and often thicker walled. The bordered pits are often twice the size of the normal (*fig. 5*).

The non-pitted parenchyma of the pericycle differs from that in the normal, in that its cells are always thicker walled and usually larger, but fewer in number. The two or three layers of cells, separating the bifurcated bundle, as well as the cells of the wedge shaped portion on the ventral side of the bundle, consist mainly of thick walled fibrous cells, which are seldom found thickened in the normal leaves (*fig. 6*).

The vascular bundle is double excepting at the base and apex of the diseased leaf. The phloem cells are larger, and the xylem cells thicker walled, than in the normal. They are not arranged as regularly in rows, and the rows, when distinguishable, are not separated by medullary rays, these being absent in the diseased leaves.

In the following table the most important differences in the structural units of the normal and diseased leaves are given:

TABLE II.

TABLE SHOWING THE COMPARATIVE ANATOMY OF THE NORMAL AND
DISEASED LEAVES OF A. BALSAMEA.

Leaf structures	Normal leaves	Diseased leaves
Cuticle.	Well developed. Smooth on outer surface, irregularly thickened on the inner, fitting closely between the somewhat irregularly thickened and projecting epidermal cells.	Cuticle present, but less developed.
Epidermis.	Cells thicker walled on outer than inner sides. Often laminated and provided with pore canals.	Epidermal cells more irregular than in normal; less thickened and seldom laminated, and provided with pore canals.
Stomata.	More on lower than on upper leaf surface. The number increases from base toward apex as the number of hypodermal cells decreases.	Like the normal, but fewer on both surfaces. Bands of stomata have fewer rows.
Hypoderm.	Well developed at basal half of leaf. Number of cells decreases from base toward apex as the number of stomata increases.	Hypodermal cells fewer, but usually larger, thicker walled and more irregular than in normal leaves. Cells often aggregated.
Mesophyll.	One to three layers of palisade cells on ventral side, rich in chlorophyll. Remaining part consists of spongy parenchyma.	No distinction between palisade cells and spongy parenchyma. Chlorophyll rarely present.
Resin canals.	Circular or nearly so. Consisting of two layers of cells — epithelial and strengthening. The latter are thick walled.	Irregular; varying in form and size, on account of the absence of the layer of strengthening cells.
Endodermis.	One layer of oblong or elliptical, thin walled cells, forming a regular ellipse bounding the mesophyll and pericycle.	Endodermis seldom distinguishable. Cells irregular in form and size. No distinct boundary between mesophyll and pericycle.

TABLE II.—*Continued.*

Leaf structures	Normal leaves	Diseased leaves
Transfusion tissue of the pericycle.	Always present. Cells have bordered pits only. Cells lignified.	Nearly always present. The lignified parenchyma cells unequally thickened. Cells have simple as well as bordered pits. Bordered pits larger than normal.
Non-pitted parenchyma of the pericycle.	Lignified parenchyma cells varying in size and thickness of their walls. Found on both sides, but mostly on the dorsal side of the bifurcated bundle.	Lignified; more irregular in form and size. Larger and thicker walled than in normal. Cells often fiber like.
Fibrovascular bundle.	Phloem and xylem consisting of from 5 to 10 rows of cells. Rows usually separated by medullary rays, the cells of which contain crystals of calcium oxalate.	Phloem and xylem less developed than in normal. The cells are often larger and thicker walled. Medullary rays and crystals of calcium oxalate are absent.

IV. ANATOMY OF THE NORMAL AND DISEASED BUDS.

1. *Normal buds.*—The buds of *A. balsamea* are conical or globular. In winter condition they are covered by a layer of resin 1 to 2^{mm} thick at the apex of the bud. The bud scales are destitute of any epidermal hairs, but the edges of the outer exposed scales, as well as the inner ones, are fringed with marginal hairs. The number of bud scales does not vary much in different buds, the smaller and lateral ones usually having the same number as the larger and terminal ones. The scales of the terminal buds are relatively larger.

The epidermal cells of the outer surface (morphologically the under surface) of the exposed scales are usually oblong, and 2 to 8 times as long as broad, usually with oblique ends. When viewed from the exterior, and in cross sections, they are found to be about twice as deep as broad, which is due mainly to the thickened outer wall of the exposed epidermal cells. This thickening of the outer wall is greater in the center of the exposed cell wall; hence, the outer wall of each epidermal cell

appears in cross sections as a protuberance from the cell. The thickened walls shows a laminated structure. The side walls are not thickened except at places where the thickening has proceeded from without inward, often unequally, so that pore canals are formed. These are best seen when the scales are mounted in chloral hydrate and viewed from the exterior. The inner wall usually remains unthickened. Variations, however, occur in the different parts of the bud scale in this and other species of Abies. Thus Schumann[12] found that in the upper part of the bud scales of *A. pectinata* the epidermal cells are thickened on all their sides. This I find takes place in *A. balsamea* also. The second, or hypodermal layer of cells, remains thin walled. The epidermis on the inner side (morphologically the upper) of the exposed scales, together with the second or hypodermal layer of cells, is usually thickened equally on all sides. The epidermal cells of the inner scales covering the growing point are thin walled like the cells of the mesophyll.

I have not succeeded in finding any stomata on the bud scales of *A. balsamea*. It is quite possible, however, that they occur, but if present, they are less frequent than in bud scales of *A. pectinata*, where I have found them, contrary to the statements made by Grüss[13] and Schumann,[14] who both say that they are never found on the bud scales of *A. pectinata*, even in a rudimentary condition.

The mesophyll or parenchymatic portion, homologous to the mesophyll of the normal leaf, is composed of from three to six layers of parenchyma cells, many of which contain chlorophyll.

The margins of the outer, as well as of the inner scales, are fringed with filamentous or hypha-like hairs (*fig. 7*). Although the marginal hairs of the outer scales are exposed to the atmosphere, they still remain thin walled, differing in this respect from the exposed epidermal cells and hairs, which always become

[12]SCHUMANN, C. G.: Anatomische Studien über die Knospenschuppen von Coniferen und dicotylen Holzgewächsen. Bibliotheca Botanica 15:3. 1889.

[13]GRÜSS, J.: Beiträge zur Biologie der Knospe. Jahrbücher f. wiss. Bot. 23:642.

[14]*Ibid.*, p. 2.

thickened and cuticularized.   Tubeuf[15] finds the marginal hairs
only on the inner scales of the buds of *A. pectinata*.   They are
present, however, and always found on the outer scales, also, not
only in *A. pectinata* but in all species of Abies whose buds are in
their winter condition covered with a layer of resin.   The mar-
ginal hairs of the outer scales are always filled with resin.[16]
With the drying of the cells of the marginal hairs, which always
remain thin walled and connected with the mesophyll, through
which the resin canals run, the resin passes from the resin
canals and inner cells to the exterior, until the bud is covered
with a layer of resin sufficiently thick to prevent any further
transpiration of moisture and exudation of resin.

The endodermis cannot be distinguished.   The central bundle
with its pericycle is composed only of a number of smaller aggre-
gated cells in the center of the scale.   No differentiation into
xylem and phloem is present.

A striking character in the structure of the bud scales of
A. balsamea is that from two to six resin canals are often present
in each scale.   The greater proportion of the scales have two
canals, the normal number of their morphological equivalents,
the leaves, but in cross sections of many scales, especially the
inner ones, one often finds in every bud some scales which have
from two to six resin canals (*figs. 8* and *9*).   As to the origin
of the increased number of resin canals, whether they are due

[15] TUBEUF : Haarbildungen der Coniferen. Forst.-naturw. Zeitsch. 1896. Son-
derabdruck S. 19 u. 21.

[16] Since the resin canals do not open to the exterior of the bud scales or any
other part of the plant, there can be no doubt but that there exists a definite relation
between the marginal hairs of the bud scales and the exudation of resin on the
buds.   It is evident that the resin, which begins to exude in the late summer and fall,
as soon as the scales begin to dry up, must diffuse through cell membranes.   That
resin diffuses through cell walls has been demonstrated (compare Grüss, *ibid.*, p.
642; Mayr, *Pop. Sci. Monthly* **28** : 680; and Harz der Nadelhölzer 80. 1894).   It
does not, however, diffuse through the cuticularized and thick walled epidermis cells
of the outer scales.

In many conifers, *e. g.*, *Picea nigra* and *P. excelsa*, whose buds are not resin-
covered, the bud scales are coriaceous and destitute of resin canals.   The marginal
hairs of the outer scales of *P. nigra* are thick walled and the inner scales seldom have
any marginal outgrowths.

to the branching of the two canals already present, or whether they are peculiar to the scales of *A. balsamea*, I am not able to state.   It appears, however, that in all species of Abies whose buds are covered over with resin in the winter, there is an increase in the amount of resin production in the bud scales over that produced in the normal leaves, and hence it is proba- ble that more than the normal number of canals can develop in the bud scales.   The resin canals are seldom surrounded by a layer of strengthening cells.

The growing point with its rudimentary leaves is covered over by the inner scales, which are imbricated, and cover the apex of the growing point four to six layers deep.   Longitu- dinal sections of the growing point show that in its winter con- dition no tissue differentiation whatever has taken place.   The central portion (plerome) has pith characters.   In cross sections no resin canals or rudimentary bundles are present.

The septum (Knospenscheide or Scheidewand), which makes the break in the pith at the annual nodes in most species of conifers, is well developed in buds of *A. balsamea*.   It consists of from six to ten layers of thick walled cells, forming a dia- phragm, separating the pith of the growing point and young shoot from the pith of the last year's internode.   Immediately below the diaphragm there is always to be found a mass of loosely connected, rounded pith cells (*fig. 10*, *f*, *g*), which in older internodes have separated from the septum, or diaphragm, so that a cavity is formed.   This empty chamber is seldom pres- ent below the septum of the bud in its winter condition.   In the spring, however, as soon as the differentiation of the peripheral cells of the plerome begins, and the xylem cells of the vascular bundle begin to elongate, the septum is partly raised above the loose tissue of the pith of the last year's internode, thus forming the pith chamber, which is always present below the septa of the first and second year old and older internodes.

Fritsch[17] found that the cells of the septum are in the form

[17] FRITSCH, CARL: Die Marklücken der Coniferen. Schriften d. Kgl. physik. Ökonom. Gesellschaft zu Königsberg **25** : 50. 1885. [Separat-Abdruck p. 6.]

of irregular three to four sided prisms, whose sides are more or less arched. In cross sections the cells appear to be pressed together in the direction of the long axis of the stem, their lumina being longest in the radial direction. The cells are about equally thickened except where the pits appear to meet, being separated only by the primary cell wall.

As has already been stated, the leaves of Picea have promi-nent pulvini at their bases. Masters[18] calls attention to the fact that the central fibrovascular bundle of the leaf passes directly from the axis into the leaf, and does not traverse the prominent swelling at the apparent decurrent base of the leaf. The pul-vini, therefore, do not form a part of the leaf, being mere out-growths from the sub-epidermal and corky layers. In buds of Picea, especially in the terminal buds,[19] these swellings or pulvini are collected into a mass surrounding the bud. On this account the bud appears swollen beneath the bud scales, which, like the leaves, have these swellings and thus aid in making the basal portion of the bud assume this fleshy character.

The same is true in species of Abies, except that the appar-ent decurrent basal swellings of the leaves are much less marked.

The terminal shoots and buds of *A. balsamea* show to a great extent the same characters as those of Picea, the buds having he characteristic swelling below the bud scales. The bud scales are also provided with thickened bases, which in their compact arrangement in the bud have lost their decurrent aspect. The basal swellings of the innermost (uppermost) bud scales, covering the sides and apex of the growing points, differ essentially in structure from the lower and outer scales in that they consist of a mass of thick walled cells, very similar in structure to the cells of the pith septum, above which they project (*fig. 10, c*). In cross sections made at the base of the septum, a ring of this col-lenchymatic tissue can be seen in the section (*fig. 10, b*). Busse[20]

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[18] MASTERS, M. T.: Note on the relation between morphology and physiology in the leaves of certain conifers. Jour. Linn. Soc. Bot. **27** : 547. 1879.

[19] Compare Tubeuf, *ibid.*, p. 19.

[20] BUSSE, W. : Beiträge zur Kenntniss der Morphologie und Jahresperiode der Weisstanne. Flora **77** : 121.

calls the ring of this tissue in *A. pectinata* the wall of the cup, the pith septum being its bottom. The wall of this cup surrounds the growing point in winter; the youngest inner bud scales grow from this annulus. That this annulus of thick walled tissue at the base of the innermost scales does not form a part of the internodal pith septal layer is shown by the fact that the xylem and phloem cells of the last year's internode extend up, and separate the septum from the basal swellings of the inner scales (*fig. 10, a*). In older internodes it is found dried up in the outer bark, together with the remains of the bud scales. The thick walled area of the basal swelling of the inner scales is composed of from 6 to 10 layers of cells of parenchymatic ori gin, shown by their pitted walls. That this annulus of strengthening cells, together with the pith septum, forms an additional protection to the bud in its winter condition, there can be no doubt.

TABLE III.

	Bud no.	Position	Diameter in mm.	No. of scales exposed	No. of inner scales	Total number of scales
Normal buds	1	Terminal on erect shoot	4	20	9	29
	2	" " " "	4½	20	10	30
	3	Axillary on erect shoot	2½	17	7	24
	4	" " " "	2½	19	8	27
	5	Terminal on lateral shoot	2½	16	8	24
	6	" " " "	3	19	7	26
	7	Axillary on lateral shoot	2	16	9	25
	8	" " " "	1½	18	6	24
Diseased buds	1	Terminal	2½	30	8	38
	2	"	2½	27	9	36
	3	"	3	29	7	36
	4	Axillary	1½	25	6	31
	5	"	1¾	27	7	34
	6	"	1½	24	6	30

2. *Diseased buds.* — The diseased buds are more numerous, shorter, and somewhat larger than the normal. They are covered with a layer of resin, and in this respect are well protected. Like the normal buds their scales have no epidermal hairs. The diseased buds are covered over with a greater number of bud scales

which are smaller than the normal. In the third table the number of exposed and of inner scales of normal and diseased buds are given.

From the above table one sees that the number of the inner scales does not vary much in the normal and the affected buds. The number of exposed scales, however, have been increased from 16 to 20 in the normal, to 24 to 30 in the diseased buds. More of the diseased scales are, therefore, provided with a cuticularized and sclerotic epidermis than the normal. The total number of scales has also been increased from 24 to 29 in the normal to 30 to 38 in the diseased.

One reason for this increase in the number of scales in the diseased buds is their relative smaller size. The buds thus require more scales to cover the growing point, which is also larger in diseased than in healthy buds.

The diseased scales, like the normal, have no stomata. The marginal hairs are present and as in the normal scales remain thin walled. Those of the outer scales are always filled with resin soon after the resin exudation begins.

The outer exposed epidermis is composed of shorter and more irregular cells than that of the normal. Cross sections of the scales show that the outer wall of the epidermal cells is thickened and cuticularized. The thickening never extends to the side or inner walls. The walls are not more than half as thick as in the normal epidermal cells. The inner, upper epidermis is rarely thickened excepting at the base of the inner scales.

The mesophyll, which is less developed than in the normal scales, consists of larger but fewer cells. The resin canals are fewer, more irregular in size and form; more than two are never present. They contain fewer epithelial cells, which vary greatly in size. Many of the diseased bud scales have no resin canals.

The endodermis, pericycle, and central vascular bundle, which in the normal scales have been reduced to a few cells, smaller than the surrounding mesophyll cells, are not found in the diseased scales.

The bases of the inner scales have the same fleshy tissue composed of thickened, strengthening, and protecting cells. This tissue, as in the normal buds, projects above the base of the young growing point. There is no difference whatever in the development of this tissue in the normal and the diseased scales.

The rudimentary leaves and apex of the growing point are larger, being composed of larger cells than the normal. This is especially true of the pith or central plerome cells. No resin canals are present in the growing point. The pith septum at the base of the growing point is composed of about the same number, and of equally thickened, but fewer pitted cells than the septum of the normal bud.

The distribution of the fungus mycelium in the diseased bud varies in the different structural units. It is always found in the mesophyll of the bud scales where the haustoria penetrate into almost every cell, except the resin canal and epithelial cells surrounding the canals. The same is true of the resin canals of the diseased leaves. The mycelium also is present in the loose pith tissue below the septum. All the remaining parts of the bud are destitute of the fungus mycelium. It is never found in the growing point and rudimentary leaves, nor in the internodal pith septum and similarly thickened cells, forming the ring of projecting tissue surrounding the growing point at the base of the inner bud scales. It is not surprising to find that the mycelium is absent in the thick walled cells of the septum, and in the annulus surrounding the lower half of the growing point, since the cells of this tissue have no cell contents whatever, nor does the mycelium penetrate the thickened cell walls. On the other hand it is surprising not to find the fungus mycelium in the growing point and rudimentary leaves, which are covered over with the inner scales. In almost every cell of these scales the actively growing fungus mycelium is present. This absence of the mycelium in the growing point is undoubtedly due to the presence of negatively chemotropic substances, or to periodic variations in the amount of starch, tannin, and

other plant products, occurring at different seasons of the year. Thus Busse[21] found that the maximum amount of starch in the growing point of *A. pectinata* occurs in May, and that from this month on there is a decrease until in the fall and winter, when the minimum is reached. He found also three different tannins in the growing point, varying in amount at different seasons of the year.

It often happens that buds are found which have been killed by the mycelial infection of the growing point. That this infection has taken place from the inner scales there can be no doubt, since the mycelium hibernates here, and infects the rudimentary leaves and young shoots as soon as they begin to develop in the spring. The mycelium is thus evenly distributed in the bark of all diseased shoots above the tumor of the affected branch. If it were not for this mycelial infection of the young shoots and rudimentary leaves by the bud scales and parenchymatic tissue of the primary cortex, healthy leaves would be found on affected branches. This never occurs. It often happens, however, especially on the witch broom of *A. pectinata* and *A. firma*, that the leaves and young shoots are not infected. They then develop like the normal. This shows that the mycelium does not spread to any great extent in the bark after the tissue differentiation has taken place. The mycelium never spreads more than 2 to 3^{mm} each year in the healthy bark below the swelling or tumor.

V. ANATOMY OF THE NORMAL AND DISEASED SHOOTS AND BRANCHES.

1. *Normal shoots and branches.*— The leader or terminal shoots depart in their general characters from the lateral, not only in the morphology and anatomy of their leaves, but also in the anatomy and morphology of their axes. The leader shoots are longer and have a greater diameter than the lateral. This greater diameter is due mainly to the greater development of the pith and primary cortex, the most important conducting tissues of the first year's internode. The vascular bundles of

[21] *Ibid.*, p. 170

the first year's terminal and lateral shoots are about equally developed. In the second year's growth, however, the vascular bundle, especially the wood of the terminal shoots, shows a decidedly increased growth over that of the lateral. Thus cross sections of the main and lateral axes taken from the same trees give the following radial widths of their principal parts:

TABLE IV.

Axes		Outer bark Epidermis and periderm	Middle bark Primary cortex	Inner bark Secondary cortex	Wood	Pith
ONE YEAR OLD	Terminal	166μ 132 220	1348μ 1494 1245	83μ 96 90	249μ 192 288	1520μ 1610 1411
	Lateral	160 249 144	830 736 256	85 84 64	224 272 119	720 800 324
TWO YEARS OLD	Terminal	260 224 230	970 980 846	240 250 215	1040 1318 1246	1440 1250 1373
	Lateral	256 225 210	800 384 348	140 128 123	640 280] 394	560 420 390

From the second year on this increased growth of the wood and secondary cortex of the main axes over that of the lateral branches continues.

Outer bark.—The terminal shoots have no epidermal hairs. The epidermis, however, of the one year old lateral shoots has numerous short, one to five-celled hairs,[22] the cells of which soon become thick walled. The cells are usually unequally thickened and pitted (*fig. 11*). The epidermal hairs of the lateral branches thus differ from the marginal hairs of the bud scales, which remain thin walled. Since the epidermal hairs

[22] Compare Tubeuf, *ibid.*, p. 35.

soon dry up and fall off, they are seldom found on two-year old
or older internodes.

The cuticle is less developed than the cuticle of the leaves.
The epidermal cells are thickened more on their outer than
inner walls. The periderm or corky layer of the outer bark of
the one year old shoots is composed of from 4 to 6 rows of
cells, but through the activity of the cork cambium more layers
are formed the second and following years. *A. balsamea* forms
cork scales only after reaching a certain age. Thus one usually
finds trees 20 to 50 years old with a smooth bark and without
any distinct cork scales. The original epidermis is still present
and can be peeled off in small scale-like layers.

Primary cortex (middle bark).— The outer part of the primary
cortex, or middle bark, beneath the peridermal layers, is com-
posed of from 4 to 6 strengthening collenchyma cells. The
greater part of the chlorophyll parenchyma remains thin walled
during the first year. Many of the cells, however, become
thick walled and sclerenchymatous. This thickening of the
parenchyma and differentiation into mechanical tissue continues
during the second and following years. The sclerenchyma
cells soon form short branches, the cell lumen of the original
cell extending into them, giving them the appearance of
branching bast fibers. Hartmann[23] calls these cells in *A. pec-
tinata* bast fibers. That they are not bast fibers is shown by
their parenchymatic origin and profuse branching. Their cell
walls are laminated and pitted. They are usually aggregated
together in nests of from 3 to 10 cells, forming areas of mechan-
ical tissue.

Many of the parenchyma cells of the primary cortex function
as secretion reservoirs for tannin and mucilage. Crystals of
calcium oxalate are seldom found in the primary cortex. The
tannin cells are scattered over the whole primary cortex, and
do not vary in size and form from the chlorophyll parenchyma
cells. The mucilage cells are spherical, ovoid, or elliptical,
and vary in diameter from 30 to 240 μ. The largest ones are

[23] *Ibid.*, p. 27.

found in the primary cortex of the older branches. They increase in size by the distention of their cell walls ; consequently the larger mucilage cells are thinner walled.

The resin canals are always lined with one layer of epithelial cells. Surrounding this layer there are always present one or two layers of collenchymatic strengthening cells. No resin canals are formed after the first year, and during the first year only in the meristem tissue of the developing shoot, where they reach their definite size as soon as the tissue differentiation has taken place. After the resin canal has reached its definite size, the epithelial lining probably loses its resin secreting function ; but its cells still remain thin walled and are able to divide, like ordinary parenchyma cells.

It is evident that with the increase in the diameter of the main axis and the peripheral growth of the bark, disturbances must occur in the resin canals of the primary cortex. As has already been stated, the primary cortex of *A. balsamea* remains alive, and is not thrown off by the formation of cork scales before the tree stems are from 50 to 100 years old. With the increase of the peripheral growth of the tree trunk, however, the resin canals are often disturbed by the cork cambium, which at places penetrates deeper into the primary cortex. Mayr[24] has demonstrated that as soon as a resin canal comes in contact with the cork cambium, the canal is filled up by the ingrowing of its epithelial cells, forming the so-called tyloses. In the development of each internode, a new system of resin canals is formed in the primary cortex, so that the canals of one internode do not connect with the canals of the adjoining internodes. The canals are always filled with an oleo-resin, so long as the formation of cork has created no disturbance in the turgescence by the loss of water from the cells surrounding the resin canals. The main resin canals are vertical and traverse the whole length of the internode. In older stems they are not always vertical, since the peripheral growth of the bark and main axis is not always

[24] MAYR, H.: Harz der Nadelhölzer; seine Entstehung, Vertheilung, Bedeutung und Gewinnung 21. 1894.

symmetrical. A part of the primary cortex, and with it the
resin canals, may be cut off by the cork cambium. This may be
only local, or include only a part of the resin canal. The part
of the canal thus disturbed is soon filled by the ingrowing
epithelial cells. It is evident that, with the intrusion of the
epithelial cells, the resin is pressed into the undisturbed part of
the canal, causing this part to distend and increase in size, by the
radial and tangential division of its epithelial lining (*fig. 10, b*
and *c*). In this way resin vesicles are formed, often two or more
in each canal. Other factors besides the disturbances due to
the cork cambium may cause tylosis; thus great temperature
variations of exposed and shaded sides of the stem, and with it
variations in the transpiration of the bark. Tylosis begins in the
resin canal as soon as the loss of water from the cells and cell
walls reaches a certain per cent. With the filling up of the
resin canal the radial and tangential division of the epithelial
cells of the resin vesicle still continues, and with it the vesicle
increases in size, receiving at the same time all or nearly all of
the resin of the original canal. Not only do the resin vesicles
contain all the resin of the canal, but also the resin which is all
the time being secreted by the tissues of the primary and second-
ary cortex. The great quantity of resin secreted by *A. balsamea*
tends also to form the vesicles, as they begin to form even in
four-year old internodes, and before tylosis has begun. With
the increase in age of the bark the vesicles increase in size, so that
in trees 20 to 100 years old the trunk of the tree always contains
the balsam vesicles in great numbers. The larger ones are
always found on the lower part of the tree trunk. They can be
seen on the outside, where they appear as swellings or blisters
on the bark. The periderm and outer part of the primary cortex
give way to the pressure of the vesicle as it increases in size by
the radial and tangential division of its lining cells. With the
increase in size of the vesicle it becomes surrounded by several
layers of cells resulting from the division of the epithelial lin-
ing cells. These become thick walled and soon break away
from the surrounding tissues of the cortex, so that older vesicles

can be detached (*figs. 12* and *13, e*).   Cross sections of one of these vesicles shows an inner thin walled layer of cells (*fig. 13, s*), surrounded by 4 to 10 layers of strengthing cells, which are elongated or stretched in the peripheral direction (*fig. 13, d*).

Secondary cortex (*inner bark*).— The medullary rays of the secondary cortex are composed of starch and protein conducting cells.   The protein conducting cells are best seen in radial sections, where they form one layer on each side of the medullary ray.   They are analogous to the protein conducting bast parenchyma of many conifers.   The starch conducting cells occupy the central part of the ray.

The bast parenchyma cells are placed end to end in single isolated rows.   Their cells are about 2 to 3 times as long as wide. The greater number are secretion reservoirs for tannin and calcium oxalate.   Usually only one peripheral row of bast parenchyma cells is formed each year.

Bast fibers are absent in species of Abies and in the Abietineæ Many of the bast parenchyma cells become thickened and sclerenchymatic.   Like the sclerenchyma cells of the primary cortex they often branch.   They are usually found in groups or nests extending the whole length of the internode.

The remaining and by far the greater portion of the secondary cortex is made up of the sieve tubes.   They are arranged in radial rows and, as in all conifers, have their sieve plates on their lateral walls.   No vertical or horizontal resin canals are present.

Wood. — The medullary rays are composed of starch conducting or normal pith cells only.   The protein conducting cells present in the rays of the secondary cortex are wanting. As in all conifers, the tracheids of the spring wood have larger lumina than the tracheids of the fall wood.   No resin canals are present in the normal wood.

Pith. — The pith adjoining the pith septum on its under side differs from the internodal pith in that it is composed of a mass of loose cells, which break away from the septum, so that in two-year old and older internodes a cavity is formed immedi-

ately below the pith diaphragm. The greater number of these cells remain thin walled. Isolated cells often become thickened but not sclerenchymatic.

The internodal pith is made up of thin walled parenchyma cells and areas of sclerenchyma. The parenchyma cells are from 2 to 4 times as long as wide. They are polygonal in cross sections and rectangular in longitudinal sections. Isolated parenchyma cells often become thick walled in older internodes. The sclerenchyma cells are cubical and smaller than the parenchyma cells. They are provided with pore canals, and the thickening often extends inward so that the whole cell lumen disappears. The cells are arranged in definite areas extending from the periphery of the pith toward the center. Many of the sclerenchyma areas extend across the pith, thus forming a kind of diaphragm of mechanical tissue which alternates with areas of thin walled parenchyma.

2. *Diseased shoots and branches.* — The normal terminal shoots differ from the lateral, not only in that they are negatively geotropic, but also in the greater or less development of their different morphological units. The diseased shoots in many respects have characters similar to the normal terminal shoots. In comparing, therefore, the anatomy and morphology of the diseased shoots with the normal, the terminal shoots should also be considered. Hartmann[25] makes a comparison of the diseased with the lateral normal branches only of *A. pectinata.*

The affected branches, like the terminal, are negatively geotropic. Cross sections of the first year's shoots show a greater development of primary cortex and pith, while the secondary cortex and wood, in proportion to the former, are less developed, about the same as that of the lateral branches. In the second year of the diseased branches changes occur, which are more marked, especially in the increased growth of the periderm, wood and secondary cortex. The wood reaches its maximum growth during the second year. This is true of all the affected branches above the tumor. At the first point of infection the

[25] *Ibid.*, p. 35.

wood continues in its greater growth in width, producing the so-called boil or tumor. The growth in width of the secondary cortex of the tumor is greater than at any other part of the affected branches. The diseased branches have a greater diameter, but are shorter than the normal lateral branches. They have a reddish color, differing from the normal branches, which are yellowish brown. Although the diseased shoots are shorter, the number of leaves does not vary much from that of the normal.

Outer bark.—The epidermis does not vary much from the normal, except that epidermal hairs are rarely present. When present the hairs are usually only one-celled, agreeing in this respect with the terminal shoots, where epidermal hairs are absent.

The periderm is more developed. It consists of from 8 to 10 rows of cells the first year, which number is greatly increased during the second and later years, when the cork cambium gradually extends inward, and finally cuts off the primary cortex. In the tumor the cork cambium often extends as far as the secondary cortex during the first year of the infection. The cork cells are larger than the normal.

Primary cortex.—The cells of the collenchyma layer under the periderm are fewer in number, as well as less thickened. The chlorophyll parenchyma of the primary cortex contains no chlorophyll, but contains, at all seasons of the year, larger quantities of starch and tannin. More of the parenchyma cells become either thick walled or sclerenchymatous. The sclerenchyma cells branch more profusely, especially in the first year's shoot. The mucilage cells are smaller, as well as fewer, and do not increase in size with the increase in age of the branch. Fewer of the parenchyma cells contain crystals of calcium oxalate, but the number of tannin cells is greatly increased.

The resin canals are present in greater numbers, and vary more in their size and form, as well as in the number and size of their epithelial cells. The second layer of cells is less thickened. Since the growth of the periderm is greatly increased, and the formation of cork layers begins earlier in the affected

branches, even in the two-year old branches, it is evident that
the resin canals are soon cut off by the cork cambium, and on
drying become functionless.   As in the normal, the resin canals
are filled up by the ingrowing epithelial or surrounding paren-
chyma cells.   This may occur in one part of the canal only,
causing the formation of resin vesicles in the part where tylosis
has not begun.   The vesicles originate in the same way as
in the normal, by the peripheral and tangential division of the
parenchymatic lining of the resin canal.   The resin vesicles
begin to form even in the first and second year diseased shoots,
increasing in size, so that in five-year old branches vesicles or
blisters are found 3 to 8^{mm} in diameter.   In five-year old normal
branches vesicles are seldom found more than 1^{mm} in diameter.
The increase in size and number, as well as the earlier formation
of the resin vesicles of the affected branches, is due mainly to
the earlier formation of cork layers and the greater resin secre-
tion.   On account of the increased growth of the bark of the
tumor, the witch broom vesicles not only reach their largest size
here, but they dry up and become functionless sooner than in
any other of the diseased branches above the tumor.   Since the
primary cortex of the tumor is earlier affected, dries up, and is
cut off by cork layers, the resin canal communication between
the diseased branches above, and the normal branch below the
tumor, is cut off or closed, even during the first or second year
of the infection.

   Secondary cortex.—The secondary cortex contains fewer sieve
tubes, which are also smaller, often only one-half as long and
broad as the normal.   The radial walls are provided with fewer
sieve plates.   The sieve plates vary in size, but are usually
smaller and more irregularly distributed.   Fewer branching,
bast fiber-like, sclerenchyma cells are present than in the normal.
The protein conducting cells of the medullary rays are absent in
the diseased bast of *Abies balsamea*.   The bast parenchyma cells
are larger and more numerous, and are usually filled with cal
cium oxalate and tannin.

   Wood.—The growth of the wood in the diseased annual rings

does not vary greatly from that of the normal.   The width of the wood cylinder in one year shoots above the tumor is about equal to that of the normal.   The second, third, and fourth rings, however, are wider than the normal.   The tracheids of the diseased wood are thicker walled.   The annual rings of the affected branches are always more irregular in their width, and are often ten times as wide on one side as on the other.   This may occur in one ring only, the following or preceding rings being equally thickened throughout.   This unequal radial width of some rings is due to disturbances in the direction of the growth of the shoot that year.   On account of the increased growth of the wood and bark, as well as the increased number of branches, the weight of the witch broom increases with its age, and more rapidly than the normal branches.   The growth of the healthy part of the witch broom branch below the tumor is also less than in the normal ones.   This part of the branch is, therefore, less able to bear the weight of the heavier affected part, and the witch broom becomes suspended, changing its position or falling on one side.   The affected branches, which are all negatively geotropic, assume during the next season their erect growth by curving upward.   On the convex side thus formed there occurs an increased growth, not only in the width of the annual ring, but the tracheids are thicker walled, rounded, and are separated by intercellular spaces, characteristic of all regulatory tissue formed in the wood of coniferous trees as a result of resistance to mechanical forces.[26]   Although the annual rings in the affected branches are as wide and often wider than the normal, they still contain fewer tracheids per square unit of surface area.   This is due to the fact that in the diseased branches more medullary rays are formed, often twice the number that are formed in the normal wood.

Resin canals, which are absent in the normal wood of *A. bal-samea*, are always present in the wood of the tumor, and are nearly always present in the wood of older diseased branches

[26] HARTIG, R.: Den anatomischen Bau des Rothholzes. Forst.-naturw. Zeitsch. —: 163. 1896.

TABLE V.

SHOWING NUMBER AND DISTRIBUTION OF THE VERTICAL RESIN CANALS IN THE DISEASED WOOD OF A. BALSAMEA.

	Cross sections	Number of resin canals in annual rings. Annual rings arranged from bark toward pith[27]																			Diameter of resin canals μ	Remarks
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
Healthy part below the tumor.	i. 6 cm below the base of the tumor.																					No resin canals present.
	II. 1 cm below the base of the tumor.																					
Boil or tumor.	III. At the base of the tumor.	11	40	5																	12–25	Mostly endings of resin canals.
	IV. 1 cm above the base of the tumor.		56	53	49	30	27	21	2												16–56	
	V. 4 cm above the base of the tumor.	18	30	39	47	84	111	104	120	105	95	58	25	26	60	77	58	47	15	8[28]	21–55	
	VI. Middle of the tumor.	10	17	13	8	11	15	21	30	45	60	44	6	2	5						24–60	
	VII. 1 cm below the apex of the tumor.	9	6	17	30	56	50	36	28	15	11	8									18–50	
Diseased branches growing from the tumor.	VIII. Base of an 18-year-old branch.																					Canals usually found in the spring wood. The peripheral rings of the tumor are narrower and contain fewer canals. With the increase in age of the tumor there is a corresponding decrease in the number of resin canals of the annual rings; but with the increase in age of the diseased branches an increase in the number of resin canals formed takes place.
	IX. 4 cm above base of branch VIII.					4		6	19	21	26	4	3		5	4						
	X. 10 cm above base of branch VIII.						7	9	13	18	11	6	8	8		6						
	XI. 20 cm above base of branch VIII.							10	16	4	7	5		3	10	9					10–35	
	XII. 1 cm above base of a side shoot of branch VIII.	14	11	8	4																	
	XIII. 10 cm above base of shoot XII.					8	4	12	9	8	11	6	4		5							
	XIV. 9-year-old branch 40 cm above tumor.					3	5	4						5	8							

[27] By arranging the annual rings from the bark toward the pith all rings that grew the same year will fall in the same column.

[28] Year of the infection.

TABLE VI.

SHOWING NUMBER AND DISTRIBUTION OF THE VERTICAL RESIN CANALS IN THE DISEASED WOOD OF A. BALSAMEA.

Witch broom	Cross sections	Number of resin canals in the annual rings, rings arranged from bark toward pith												Diameter of resin canals μ	Remarks
		1	2	3	4	5	6	7	8	9	10	11	12		
A.—With 21 diseased branches growing from an area of about 6 sq. cm. of the tumor.	I. Healthy branch 4cm below base of tumor.														No resin canals present.
	II. At the base of the tumor.	4	19											10–40	Endings of resin canals.
	III. 1cm above the base of the tumor.	20	25	15	30	12	18[29]							11–45	Mostly endings of resin canals.
	IV. Base of a 6-year old branch from tumor.														} No resin canals present.
	V. 3cm above the base of branch IV.														
	VI. 10cm above the base of branch IV.														
	VII. 20cm above the base of branch IV.														
	VIII. 40cm above base of lateral branch of branch IV.														
B.—Growing from the top of the main axis of the affected tree.	I. Healthy part 12cm below base of tumor.														No resin canals present.
	II. Base of tumor.	7	16	9	4									8–37	Mostly endings of canals.
	III. 2cm above base of tumor.	10				4			3		4			10–40	Many of them are endings of the tumor canals.
	IV. Base of a 3-year old branch from tumor.														} No canals present.
	V. Base of a 6-year old branch from tumor.														
	VI. 4cm above base of branch V.														

[29] Year of the infection.

above the tumor.   The distribution and number of resin canals
are given in tables V and VI.

Resin canals are never found in the healthy part of the
branch below the tumor.   They first appear in sections made
at the base of the tumor and here only in the outer annual
rings.   All the resin canals of the tumor have their endings
at the base, between the healthy and the diseased wood.
The ends are pointed and gradually disappear between four
tracheids, which in their meristematic condition probably func-
tioned as epithelial cells.   In sections made above the base of
the tumor, the number of annual rings affected as well as the
number of canals increases.   The greatest number is found in
the middle of the tumor (table V, section VI), where the canals,
also reach their greatest diameter.   From the middle of the
tumor toward its apex the number of canals decreases, the
greater number of them ending at its upper end.   Many of the
canals continue in the affected branches for some distance.   The
affected branches of some witch brooms have no canals (table
VI, A., sections IV to VIII.)

Usually, however, with the increase in age of the branch,
there is a corresponding increase in the number of its canals.   With
the increase in age of the witch broom the outer annual rings of
the tumor and branches become narrower, often having only a
few layers of tracheids.   With this decrease in width of the
annual rings, there is a corresponding decrease in the number of
canals formed in the tumor ; but an increase occurs in the num-
ber of canals formed in the branches (table V, sections VI and
XII to XIV).

The resin canals are usually found in the spring wood, where
they form a ring of canals separated only by the medullary
rays (*fig. 14*).   This ring of canals sometimes extends the
whole distance around the annual ring.   Usually, however, it
extends only one-fourth to one-half of the distance, with here
and there an isolated canal.   Rings of canals and isolated
canals are often found in the summer and fall wood.   The
regulatory tissue, or so-called "red wood," formed on the

convex side of recurving branches, seldom contains any resin canals.

Pith.—The diseased pith differs essentially from the normal in that its cells become thickened sooner, also forming larger groups of sclerenchyma cells. The cells of the pith area below the pith septum, which remain thin walled in the normal branches, become thickened in the diseased branches. Small areas of sclerenchyma cells are sometimes formed, which are never present in the normal. The internodal pith shows a greater development of mechanical tissue than in the normal branches. The diseased branches, which are correspondingly larger than the normal, also have a greater development of pith.

SUMMARY OF THE MOST IMPORTANT CONCLUSIONS.

Normal organs.

1. Stomata are found in greater numbers toward the tips and on the lower surfaces of the leaves of the lateral shoots. The leaves of the terminal shoots have their stomata distributed about equally on all sides.

2. Hypodermal strengthening cells are always present in the leaves. They are seldom found in cross sections made above the middle of the leaves of the lateral branches. Below the middle they are usually found isolated on the upper leaf surface and in continuous layers on the lower surface. The shorter, rigid, and terete leaves of the terminal shoots have a greater development of hypoderm.

3. The number of hypodermal strengthening cells decreases from the base toward the tip of the leaf; but with the decrease in the number of hypodermal cells there occurs a corresponding increase in the number of stomata.

4. The transfusion tissue is not as well developed in the leaves of the lateral branches as in the leaves of the terminal shoots. In the former there are two small areas, each one lying dorsal to the outer half of the two phloem areas. In the leaves of the terminal shoots the two transfusion tissue areas have

united and formed one large area on the dorsal side of the phloem and pericycle beneath the endodermis.

5. No epidermal hairs are present on the bud scales. All the scales are fringed with thin walled, hypha-like, marginal hairs, through which the resin diffuses to the exterior of the scales, until the bud is covered with a layer of resin sufficiently thick to prevent any further transpiration of moisture and exudation of resin.

6. Resin canals are usually present in all of the bud scales. Cross sections of many scales show from two to six resin canals.

7. The terminal or leader shoots, have no epidermal hairs. Epidermal hairs are present only on the one to three-year old lateral shoots.

8. Resin vesicles or blisters are formed only in the primary cortex and in those parts of the original resin canals which have not been disturbed by the unequal peripheral growth of the bark, cork cambium, and the formation of tyloses. The vesicles originate and increase in size by the radial and tangential division of the lining cells of the undisturbed part of the resin canal.

9. The normal wood of *A. balsamea* contains no resin canals.

Diseased organs.

10. Fewer stomata are present on the diseased leaves, and their distribution is similar to that of the normal.

11. Hypodermal strengthening cells are present, especially in the basal half of the leaf; they are more irregular in their form and size ; and are often found in nests and groups.

12. The transfusion tissue is nearly always present, often in one to three small areas on the dorsal side of the phloem. The cells of the diseased transfusion tissue usually have simple as well as bordered pits.

13. The diseased buds are covered over with a greater number of bud scales, which are smaller than the normal. The diseased scales, like the normal, are fringed with marginal hairs and the buds are resin covered in winter.

14. Fewer of the diseased scales have resin canals; more than two canals are never present.

15. Epidermal hairs are rarely present on the diseased shoots. When present they are usually only one-celled.

16. Resin vesicles begin to form even in the first and second year diseased shoots. They increase in size so that in five-year old branches vesicles or blisters are found 3 to 8^{mm} in diameter. In five-year old normal branches vesicles are never found more than 1^{mm} in diameter.

17. Resin canals are always present in the wood of the tumor, and are nearly always present in the wood of older diseased branches above the tumor. The canals are usually found in the spring wood. With the increase in age of the tumor, there is a corresponding decrease in the number of resin canals of the annual rings, but with the increase in age of the diseased branches an increase in the number of resin canals of the annual rings takes place.

In conclusion, I wish to state that I am indebted to Director William Trelease and to the other officers of the Missouri Botanical Gardens for the use of their libraries and laboratories, and for kindly supplying facilities which have made it possible to do the work here presented.

MISSOURI BOTANICAL GARDEN.

EXPLANATION OF PLATES XIV AND XV.

FIG. 1. Cross section of a normal leaf 4^{mm} above its base, showing epidermal and hypodermal cells.

FIG. 2. Cross section of a normal leaf, showing the non-pitted, lignified parenchyma of the pericycle, bounded on its dorsal side by the endodermis.

FIG. 3. Cross section of a normal leaf, showing one of the two areas of transfusion tissue.

FIG. 4. Cross section of a diseased leaf, 4^{mm} above its base, showing the epidermal and hypodermal cells.

FIG. 5. Cross section of a diseased leaf, showing two areas of transfusion tissue: *a*, non-pitted, lignified parenchyma; *b*, bordered pits; *s*, simple pits.

FIG. 6. Section of diseased leaf, showing non-pitted, lignified parenchyma. Same magnification as in *fig. 2*.

FIG. 7. One of the outer and exposed normal bud scales, fringed with the marginal hairs, which are thin walled and filled with resin.

FIG. 8. Cross section of a normal bud scale with four resin canals.

FIG. 9. Cross section of a normal bud scale with two resin canals.

FIG. 10. Longitudinal section at the base of a bud of a normal shoot: *a*, cambium, with phloem and xylem cells; *b*, base of the annulus, or wall of the cup, surrounding the growing point in winter; *c*, base of the inner bud scales, composed of thick walled collenchymatous cells, similar to those of the annulus and pith septum; *d*, parenchyma of the primary cortex; *e*, part of pith septum, with irregular 3–4-sided prismatic cells; *f*, pith cells; *g*, loosely connected rounded pith cells, which break away from the septum in older internodes, forming the pith chamber.

FIG. 11. Epidermal hairs on a normal one year old lateral shoot.

FIG. 12. One of the detached resin vesicles of the primary cortex, magnified about four diameters: *a*, remnant of the original resin canal from which the resin vesicle developed.

FIG. 13. Cross section of the thin membrane covering the resin vesicle : *a*, thick walled, elongated or stretched cells of the membrane; *s*, thin walled epithelial cells lining the membrane of the vesicle on the inside ; *b*, one of the epithelial cells dividing radially ; *c*, one of the epithelial cells dividing tangentially ; *d*, primary cortex ; *e*, parenchyma cells of the primary cortex torn loose from the resin vesicle membrane, which has elongated or increased in size peripherally.

FIG. 14. Cross section of the wood of a diseased branch about 1^{cm} below the middle of the tumor, showing two abnormal vertical resin canals : *a*, an in-grown epithelial cell, filling up almost the entire lumen of the resin canal (tylosis).

PLATE XIV.
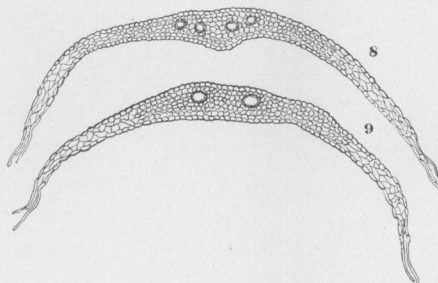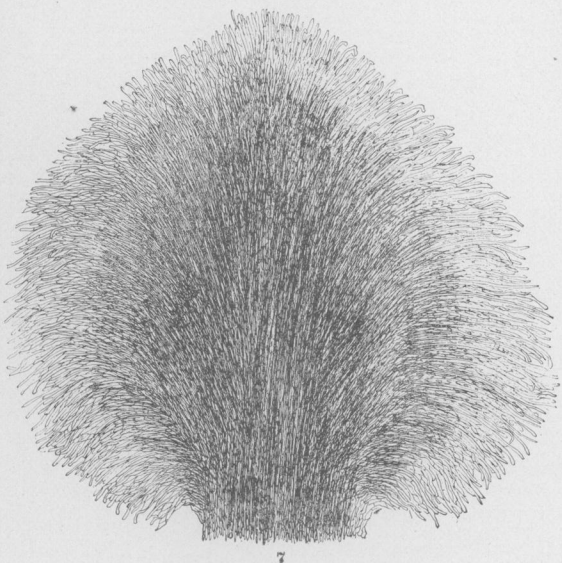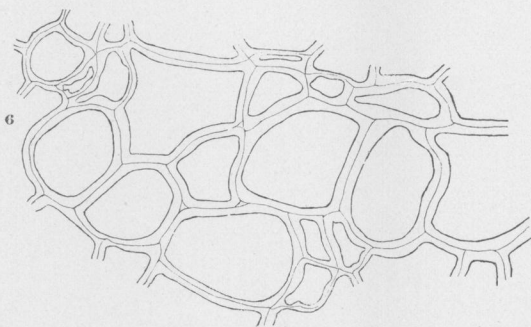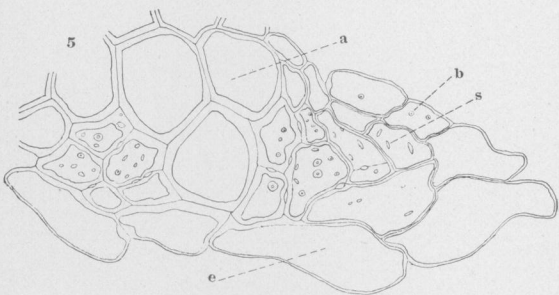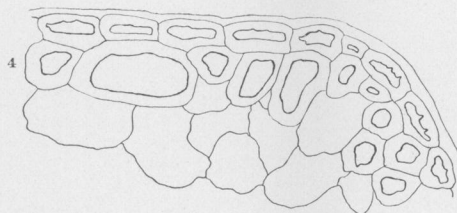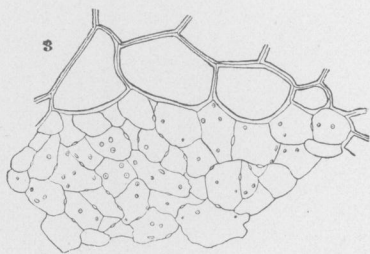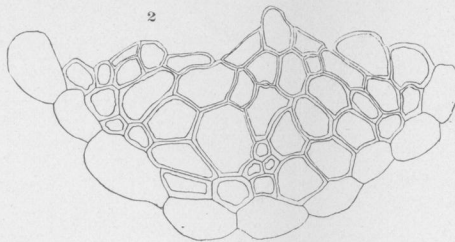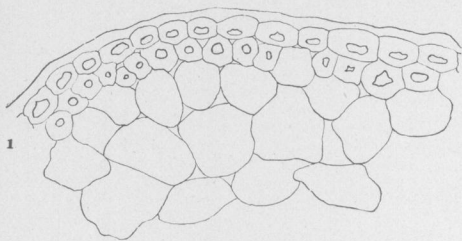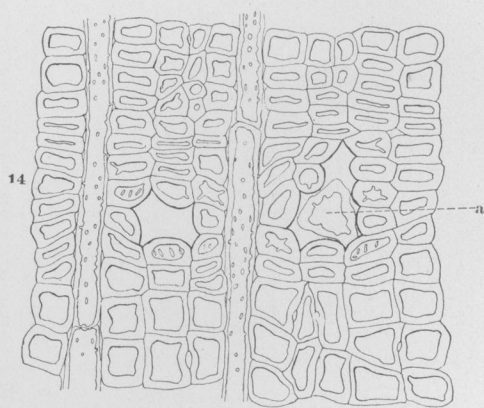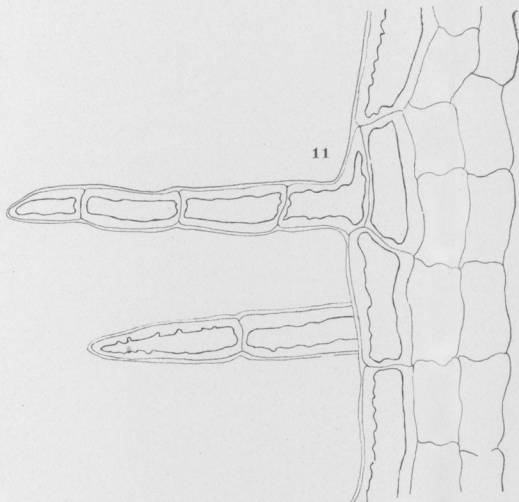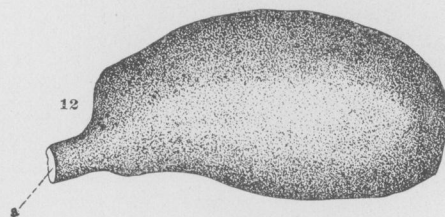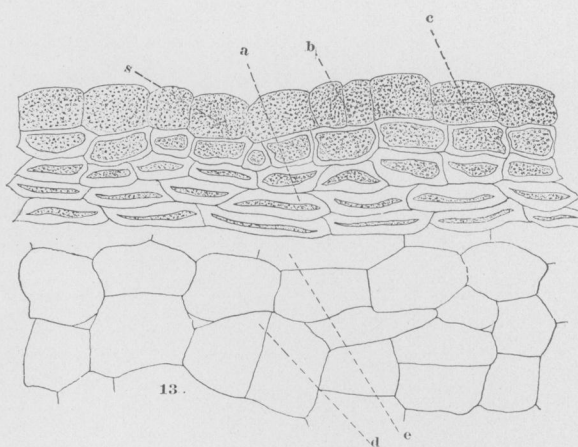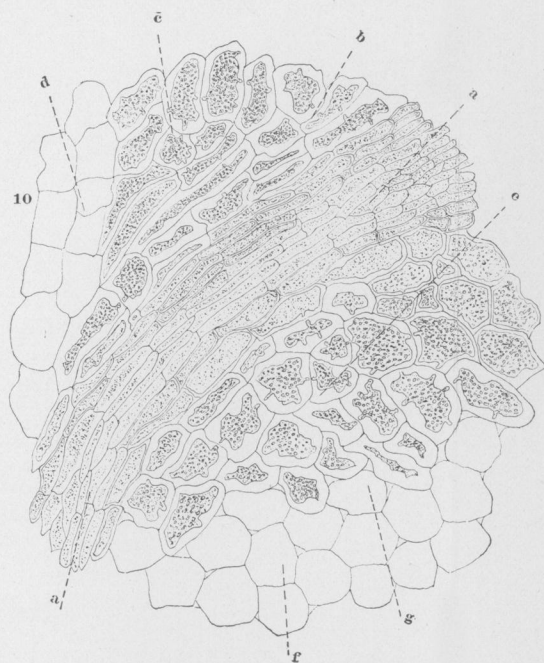
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